EFFECTS OF ENFORCED WAKEFULNESS UPON THE GROWTH AND THE MAZE-LEARNING PERFORMANCE OF WHITE RATS

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The familiar admonition to "get more sleep" reflects a presumption that loss of sleep is deleterious. This presumption is substantiated by experimental investigations which have shown that prolonged, uninterrupted deprivation of sleep leads, in human beings, to hallucinations and to other evidences of mental disorganization (1, 9, 13, 14, 16). Animal subjects have, indeed, been kept awake until they collapsed and died (3, 6, 10, 17).

But in everyday life loss of sleep is rarely both prolonged and uninterrupted. It is more usual for an individual to miss sleep entirely for a night or two, or to persist for a longer period of time in getting somewhat less than the "normal eight hours." Of special interest, therefore, are the effects *first* of complete deprivation for short intervals, on which the experimental literature is substantial (see 11), and *second* of partial deprivation for long intervals, on which the present study is one of few.

In the other experiments on partial deprivation (7, 12), human subjects were used, and relatively minor variations in sleep pattern were studied. In the present experiments, interest centered upon maximum tolerable deprivation, and white rats were used as subjects.

The aims of the experiments were to determine how little sleep would actually suffice for white rats, which normally sleep 12 to 15 hours a day, and to note the effects of keeping them, for an extended period, on a regime which allowed them only a minimum amount of sleep. The effects upon growth and upon maze-learning ability were of primary concern.

Two questions presented themselves immediately. How does one decide whether a white rat is awake or asleep? How can a number of rats be kept in a condition which meets the criterion of wakefulness? The first question tends, of course, to become philosophical, and the answerer to become pragmatist: a rat is awake when its head is up and its eyes are open. The second question leads to experiment. It was found that rats cannot be kept awake for long periods by placing them on beds of nails (cf. 15), by playing upon their negative phototropisms with bright lights, by disturbing them with sound, or by making them balance on precarious perches. Thus it appeared that Kleitman was quite correct in saying (10, p. 646):

> It must be borne in mind that in all experiments prolonged wakefulness, both in man and in animals, could be accomplished only at the price of continued muscular activity.

As a means of enforcing continued muscular activity, a motor-driven revolving cage was an obvious choice, but Bast and Loevenhart (2) had used revolving cages and had found that some of their rabbits had simply gone to sleep and let the apparatus roll them over and over. It was decided, therefore, to try a motor-driven treadmill surrounded by water. If the rats went to sleep, they would be dumped off the end of the treadmill into the water, immersion would awaken them, and they would scramble back onto the treadmill.

The treadmill surrounded by water proved to be quite effective as an arrangement for enforcing wakefulness. The rats, placed together on the treadmill moving at approximately a foot a minute, were intermittently active, keeping their heads up and their eyes open. It was noted with some surprise that the rats did not hurry to the front end of the treadmill to catch naps in transit. Instead, they tended to bunch together in a group and to climb upon one another's backs. This activity was perhaps even more effective in keeping them awake than was the activity enforced directly by the treadmill.

MAXIMUM TOLERABLE DEPRIVATION

In order to find out how much sleep white rats require, a preliminary experiment was conducted with four groups of rats (N's = 5) from the laboratory colony: one group was kept awake 12 hours each day, another 16, a third 20, the fourth 24, and observations were made to see how the several groups fared with the passage of time. The rats of the 24-hour group were kept on the treadmill without intermission (except for daily inspection and weighing) until they died, which they did after periods of from 3 to 14 days. Most of the deaths resulted, not directly from loss of sleep *per se*, but from fighting. The rats of the 24-hour group became so hypersensitive (or hyper-reactive) that even slight physical contacts precipitated vicious, aggressive behavior. This behavior was not always directed against the actual offender, and occasionally several innocent rats would become involved in a fight while the original aggressor stood by and watched.

The 12-, 16-, and 20-hour groups which were removed from the treadmill each day for rest periods of 12, 8, and 4 hours, respectively, were affected much less severely than was the 24-hour group. One rat of the 16-hour group died after a fight, but the 12- and 20-hour groups had suffered no losses when the preliminary experiment was terminated at the end of three weeks. The rats that were kept awake 20 hours a day became extremely irritable, but it appeared that they could have continued indefinitely with only four hours a day for sleep. Therefore, the 20-hour wakeful regime was chosen as the principal condition in the main experiment. In order to avoid a repetition of the fighting, however, it was thought advisable to isolate the rats in individual cells in the apparatus used to enforce wakefulness.

THE PLAN OF THE MAIN EXPERIMENT

Because factors other than wakefulness *qua* wakefulness were introduced into the experiment by the method of enforcing wakefulness, three control groups were used. These were: (1) a *cell* group, which occupied cells in the activity-enforcing apparatus just like those in which the wakeful group was kept except that the treadmills were stationary; (2) an *exercise* group, which also occupied cells in the apparatus and which was forced to cover in an hour and forty minutes each day the distance travelled by the wakeful rats in 20 hours; and (3) a *laboratory* group, composed of rats living in the regular laboratory cages. Rats were assigned to the wakeful group and to the three control groups at age 20 days. Each litter was divided among the groups, and the ratio of males to females was made as nearly as possible the same for all the groups.

From *age 20 days* until the experiment was terminated, the rats were weighed at intervals of approximately two days. At *age 30 days*, the groups were placed on their respective regimes. At *age 50 days*, daily trials were begun on a difficult escape-from-water maze. These trials were continued for each rat until it swam the maze without error on three successive days.

Toward the end of the experiment, three rats of the wakeful group and two of the laboratory group were placed in an activity-recording apparatus in order to find out whether or not the wakeful rats, having been deprived of sleep, would spend more time at rest than would the controls. When the first rats selected for the experiment had lived under the experimental conditions for 123 days and the last rats for 73 days, the experiment was terminated by putting some of the rats back into regular laboratory cages for observation and by placing the remainder on a 24-hour wakeful regime which was continued until the rats collapsed.

APPARATUS

Enforcement of wakefulness

The apparatus used in keeping the rats awake is shown in figure 1. Of the four rows of cells, two were used for the wakeful group, one for the exercise group, and one for the cell group. In each cell there was a small treadmill, four and one-half inches in diameter and three and one-half inches wide. The treadmills to which the rats of the wakeful group were assigned were turned approximately seven and one-half inches per minute for 20 hours each day; those for the exercise group were rotated 12 times as fast for one-twelfth as long; those for the cell group were locked so that they could not be rotated. The rats of the wakeful group had to move at least once every ten or fifteen seconds to keep from getting wet.

The food compartments, which were within easy reach of the rats standing on the treadmills, always contained six-gram checkers of Purina Chow. The rats drank from the water which surrounded their treadmills. The water was changed at frequent intervals. Constant illumination was provided by two 200-watt bulbs above the apparatus.

Maze learning

The learning problem was a 14-unit escape-from-water maze, the pattern of which is shown in figure 2. The water in the maze was about 8 inches deep—

deep enough to force the rats to swim. The correct route through the maze was 196 inches long from the entrance chute to the exit ladder and involved 14 turns. At alternate choice points, there were doors which could be lowered to prevent retracing. Dummy doors, located symmetrically, kept the functional doors from serving as visual cues. A large mirror, placed above the maze at an angle of approximately 45 degrees, enabled the experimenter to observe the movements of the rat without leaning over the maze. The maze was illuminated by the light from two 200-watt bulbs reflected downward from the mirror and was set off from the rest of the laboratory room by a black drape.

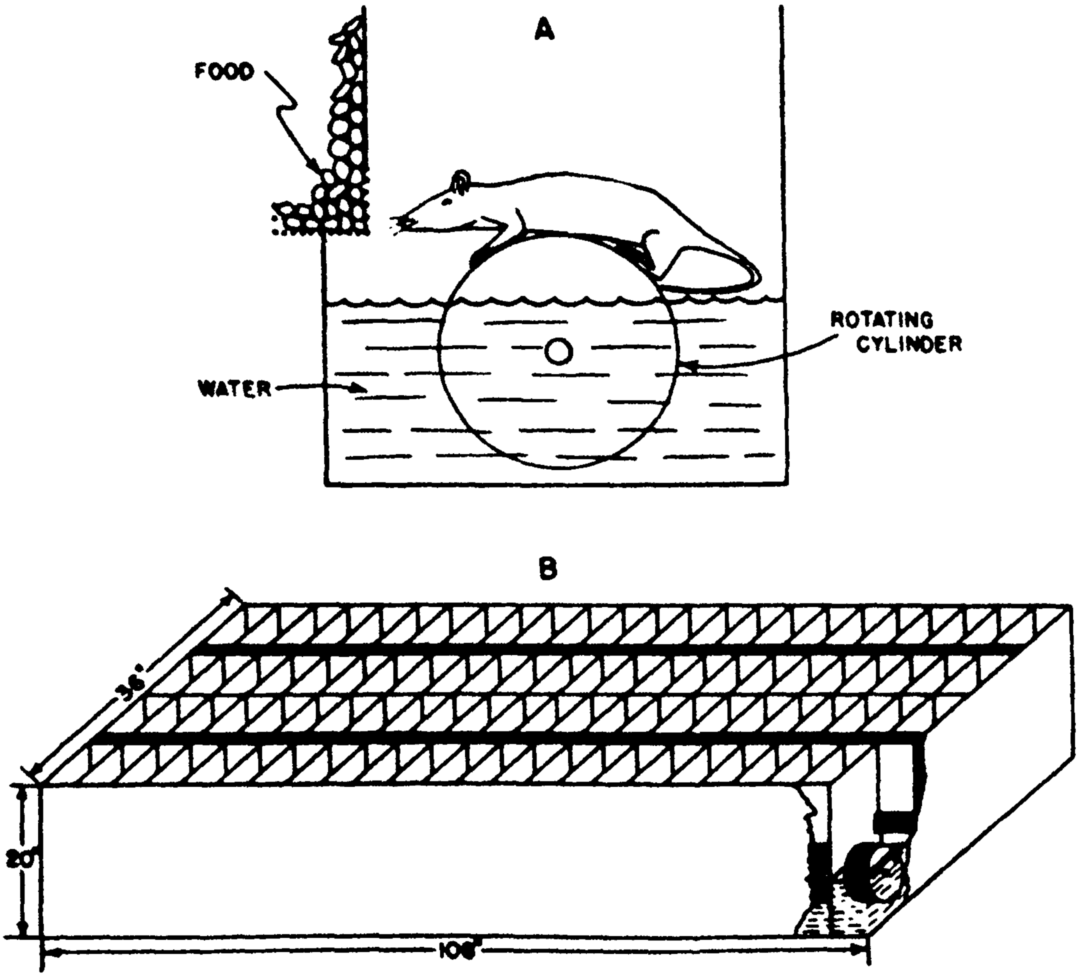

FIG. I

FIG. 1. APPARATUS USED TO ENFORCE WAKEFULNESS

A shows schematically the arrangement within an individual compartment. *B* is an oblique drawing of the overall apparatus. The rats of the *wakeful* group were quartered in the first and third rows of compartments. The *cell* group was assigned to the second row, and the *exercise* group to the fourth.

The following data on the maze performance of each rat were recorded: (1) Time, as measured by stopwatch from the moment the rat hit the water until it passed under the last door. (2) Distance, as determined by noting the movements of the rat past distance markers located at two-inch intervals along the tops of the walls of the pathways. (3) Errors, assigned whenever a rat entered a blind T-stem or a blind T-end or moved more than a body length in the wrong direction in a correct pathway. (4) Speed of swimming, as determined for each trial by dividing the total distance traversed by the duration of the trial. (5)

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Activity recording

It had been found previously by Bunch that the cycles of activity indicated by records of a rat's movements in an activity cage coincided with the temporal pattern of wakefulness and sleep as judged by direct observation. Since it was of interest in connection with the present experiment to determine whether or not rats sleep more than usual after partial deprivation of sleep, an activity-recording apparatus, similar to one which Bunch had used, was employed.

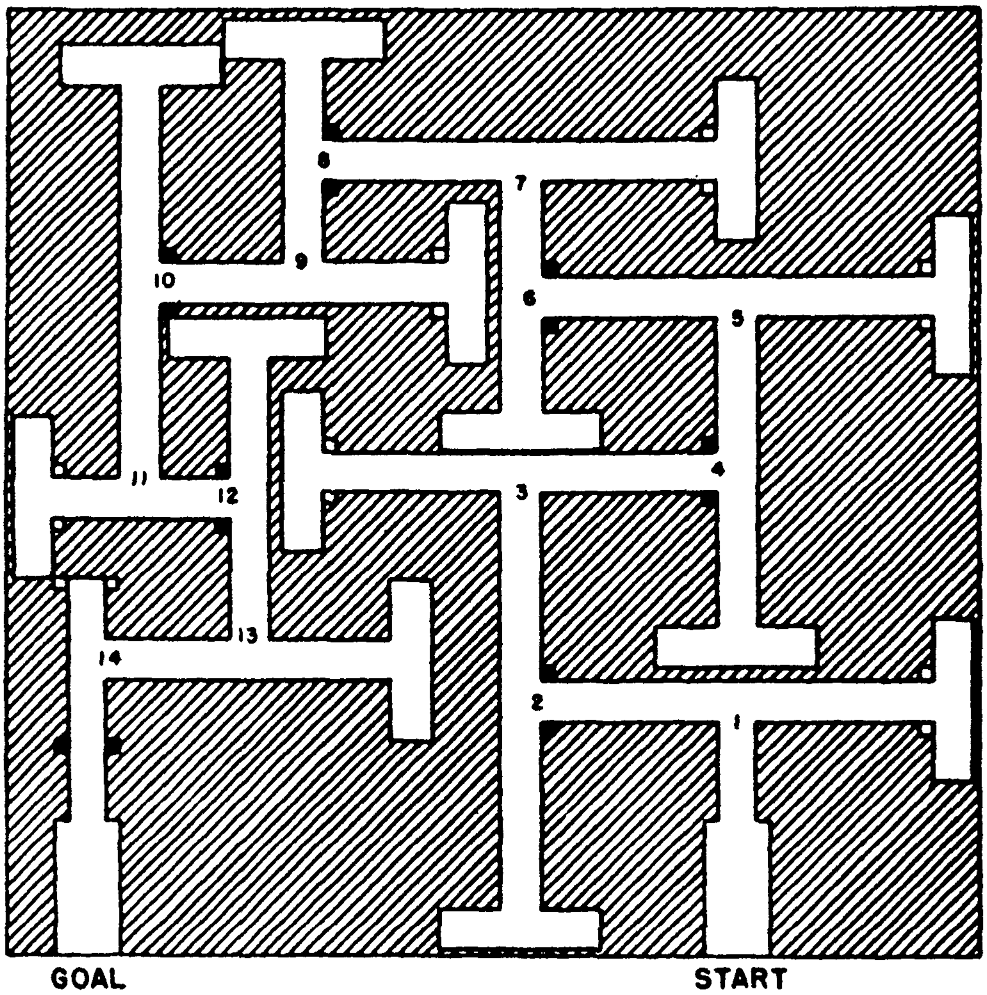

FIG. 2

FIG. 2. ESCAPE-FROM-WATER MAZE

The 14-unit multiple-T pattern is a modification of a design used by Stone. The filled squares indicate the locations of functional doors used to prevent retracing. The unfilled squares indicate the locations of dummy doors. Water filled the maze to a depth of approximately 8 inches.

The apparatus consisted of a cage with a spring-suspended floor and means of recording movements of the floor through variations in the capacitance of a condenser, one plate of which was attached to the floor. This apparatus was located in a quiet room with constant illumination.

RESULTS

Effects of the enforced wakefulness were observable within a few days after the experimental conditions were put into force. The wakeful rats fell behind in [illegible], and appeared to become more irritable than the controls. The rats in the cell and exercise control groups adjusted readily to the conditions under which they were forced to live. No unusual circumstances affected the animals of the laboratory group.

Of the 158 rats selected for the experiment, 11 died between the ages of 30 days and 50 days (i.e. between the beginning of the experiment and the first trial in the maze); none died during the maze trials. Of the 11 deaths, only four were in the wakeful group; these reduced the number of wakeful subjects from 52 to 48. Three deaths occurred in the cell group (N from 24 to 21), one in the exercise group (N from 24 to 23), and three in the laboratory group (N from 58 to 55).

As the experiment progressed, the wakeful rats became increasingly aggressive; by the thirtieth day it was necessary to use heavy gloves in handling them. After about 40 days with only four hours a day for rest, however, some of the wakeful rats appeared to reach their limits of tolerance. Several of them lost weight rapidly and died. The others grew scrawny in appearance and became almost vicious in their behavior.

Growth curves

Curves showing weight as a function of age are presented in figure 3. Mean values are plotted separately for the male rats and the female rats. In each plot, the curve for the wakeful rats falls below the curves for the controls, showing that the enforced wakefulness reduced the rate of growth. The differences in weight between the wakeful and the control groups had become statistically significant at the one-percent level by the time the experimental conditions had been continued for ten days; they remained highly significant throughout the course of the experiment.

Inspection of the curves indicates that:

(1) Until the actual experimental conditions were put into effect (when the rats reached age 30 days), the mean weights for the four groups follow very similar courses.

(2) Between age 30 days and age 70 days, the wakeful rats grew less rapidly than the controls but were able, nevertheless, to add weight at an appreciable rate.

(3) At age 72 days, the rate of growth of the wakeful rats suddenly dropped almost to zero. This effect was not due to deaths of heavier-than-average rats: actually, the few animals that died near age 70 days were nearly average in weight until, as described above, they broke down under the stress of enforced wakefulness. Nor was the effect due to any factor which might have disrupted the experiment at a particular time: the various litters reached their seventieth days of age at intervals over a period of seven weeks.

(4) The growth curves for the male rats of the cell, exercise, and laboratory groups followed almost identical courses; the growth curves for the female rats of the control groups were somewhat more divergent.

Maze performance

In handling the rats, and especially in retrieving rats which were able to escape occasionally from the experimenters, it was noted that the wakeful rats reacted much more vigorously than did the control rats. As soon as the maze trials were started, a similar difference appeared in the reactions to the escape-from-water problem. The wakeful rats swam faster and were more continuously active than the controls. As the trials progressed, it became evident that the effect of enforced wakefulness upon performance in the maze was by no means deleterious. In all of the aspects of maze performance which were measured, the wakeful rats were superior to the controls. In this respect, the results of the present experiment were similar to those of previous experiments reported by Bunch, Cole, and Frerichs (4) and by Bunch, Frerichs, and Licklider (5). In these earlier experiments, groups of white rats had been kept awake for 8, 16, 24, and 48 hours and immediately thereafter had been given massed practice in a maze. The wakeful rats had learned the maze more rapidly, in fewer trials, and with fewer errors than had the controls.

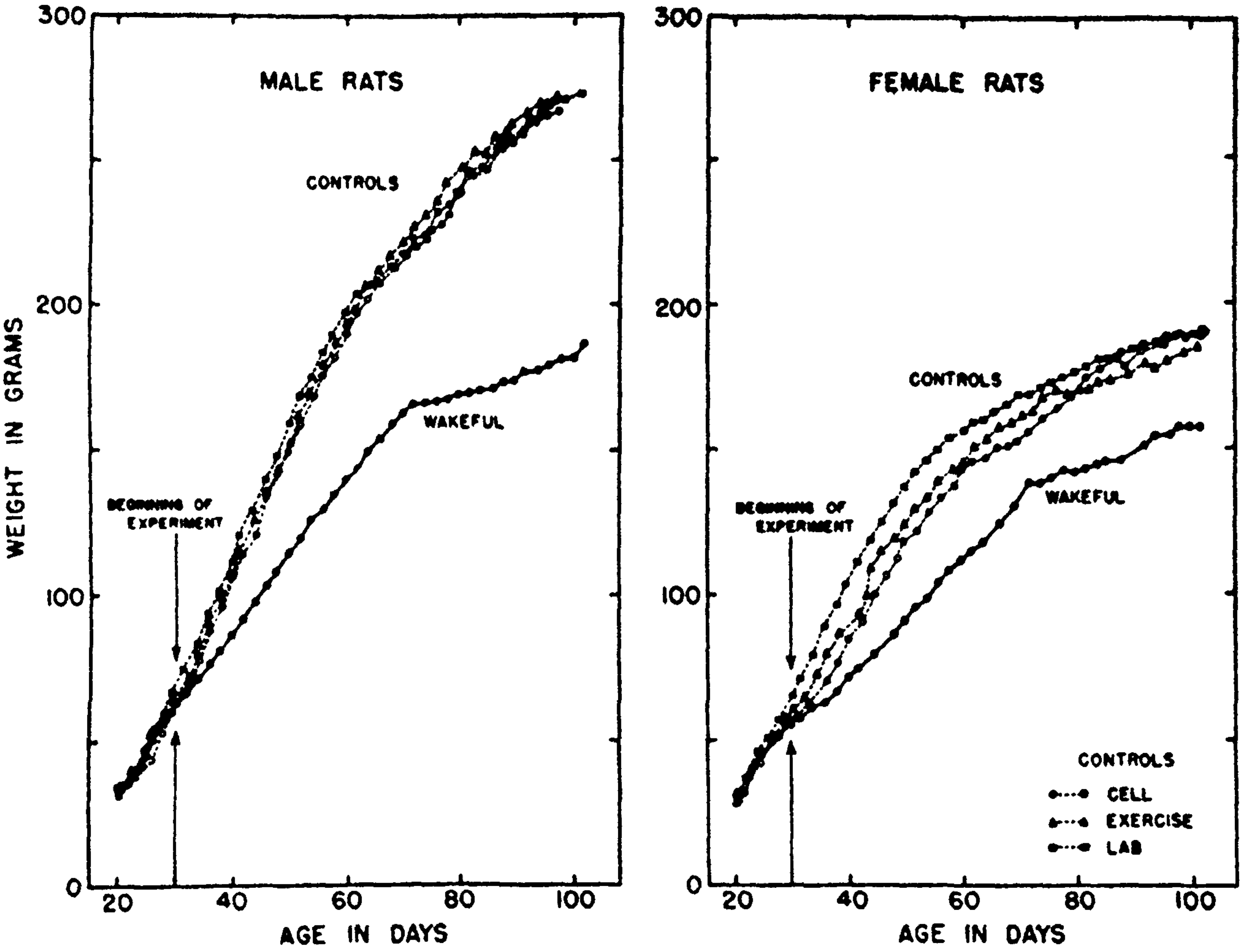

FIG. 3

FIG 3. GROWTH CURVES

The curves relating mean weight to age show that the wakeful rats grew less rapidly than the controls. The wakeful group fell behind as soon as the experimental conditions were put into effect. After 40 days of partial deprivation, the wakeful group showed a second decrement in rate of growth.

In the present experiment, however, the superiority of the wakeful rats may be regarded primarily as one of performance and not, insofar as the distinction can be made, one of ability to learn. As will be evident from the more detailed description of the results which follows, the better performance of the wakeful rats is largely to be accounted for in terms of their more aggressive behavior.

Curves showing, for each of the groups, the trial-by-trial decline of the time, distance, and error means are presented in figure 4. These curves indicate that the superiority of the wakeful rats did not manifest itself clearly in the first few trials but that it became rather consistent during the latter part of the maze practice. The margin of superiority appears considerable when performance is quantified in terms of time, but the differences between the distance and error means for the wakeful and control groups are relatively small.

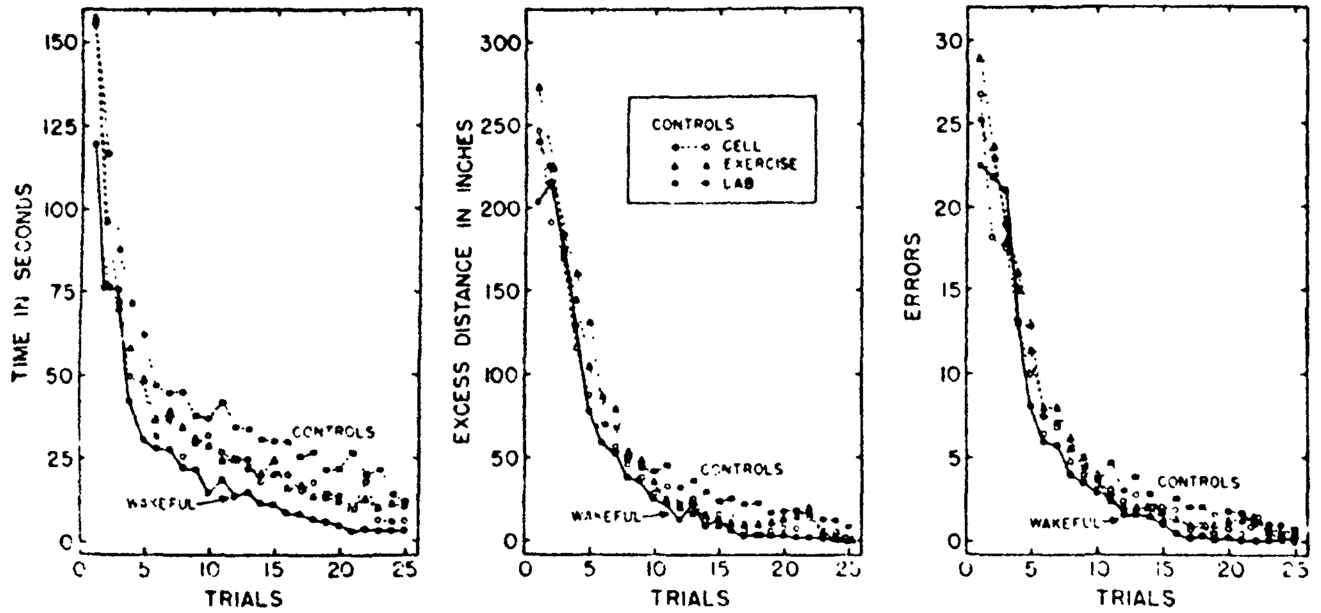

FIG 4

Fig. 4. Curves Showing the Progress of Maze Learning from Trial to Trial

The datum points are group means. Although the differences between the groups are considerable only in the case of the time scores, it is clear that the wakeful group was rather consistently superior to the control groups, especially during the latter trials, with respect also to distance traversed in the maze and to errors.

The maze results are summarized in table 1, which gives the mean overall scores for each of the groups. It is notable that within the table there is not a single inversion of the rank order: wakeful, cell, exercise, laboratory. Not all of the differences between groups are significant, however. Estimates of the significances of the differences are given in table 2. These estimates, which must be regarded as approximate because the distributions were not entirely normal, are in the form 1-P, where P is the probability that the means of the two groups under comparison would differ as much as they did simply as the result of errors of random sampling.

Inspection of the tables indicates that prolonged partial deprivation of sleep through the method used in the experiment makes white rats swim faster. This is directly evident in terms of speed of swimming and reflects itself, also, in the time scores. It is in line with the general picture of vigorous, aggressive behavior on the part of the wakeful rats.

It is also evident from inspection of the tables that whether or not other conclusions may be drawn as to the effects of enforced wakefulness upon maze performance depends to a considerable extent upon which of the three control groups is considered the "normal" one. The wakeful group required fewer trials for mastery, made fewer errors, and traversed less excess distance in learning the maze than did the control groups, but in these terms its superiority over the cell group was not statistically significant. The cell group, in turn, outperformed the exercise and the laboratory groups, but only its superiority over the laboratory group was significant. Thus it might be concluded that both enforced wakefulness and solitary confinement without exercise lead to improved maze performance, but that the effects of wakefulness are somewhat more marked. On the other hand, the cell group might be chosen as the reference group, and it might be argued that the effects of enforced wakefulness manifest themselves primarily in terms of time scores and in speed of swimming.

TABLE 1

Maze performance

GROUP	N	TRIALS	ERRORS	DISTANCE	TIME	SPEED
				in.	*sec.*	*in./sec.*
Wakeful	48	17.3	124	1188	598	4.28
Cell	21	19.1	132	1254	836	3.42
Exercise	23	24.6	153	1454	930	3.42
Lab	55	26.0	172	1680	1247	3.08

TABLE 2

Statistical significance of group differences

GROUPS	TRIALS	ERRORS	DISTANCE	TIME	SPEED
			in.	*sec.*	*in./sec.*
Wakeful—Cell				.98	.99
Wakeful—Exercise	.95	.99	.99	.99	.99
Wakeful—Lab	.99	.99	.99	.99	.99
Cell—Exercise					
Cell—Lab	.95		.99	.99	
Exercise—Lab				.95	

Finally, the possibility cannot be denied that the differences between the groups in maze performance may to some extent simply reflect differences in strength of escape-from-water motivation. It will no doubt have been noted with some uneasiness that there was a large amount of water in the maze and a large amount of water in the activity-enforcing apparatus. In the laboratory cages, there were only small dishes of water for the rats to drink. After living for several weeks with water as a constant threat, the rats which were kept in the apparatus may have developed habits of withdrawing from water, and these habits may have influenced their behavior in the maze. It should be noted, however, that the wakeful rats were observed to be more active and more aggressive than the controls in other situations (e.g. weighing) which did not involve escape-from-water motivation.

An unusual item of behavior, which appears to be of possible significance in connection with the problem of the motivation of maze learning, was noted during the maze trials of two rats of the wakeful group. These rats on at least two occasions climbed from the goal box back down into the maze, after completing their runs, and swam through the pathways in reverse order. One of them, having just turned in the best performance of the experiment by making perfect runs on its third, fourth, and fifth trials, swam back through the pathways until it met the rat next in sequence, then turned around and negotiated the final one-third of the maze at high speed.

TABLE 3

Activity records

GROUP	RAT	PERCENTAGE OF TIME INACTIVE		NUMBER OF CYCLES OF ACTIVITY—INACTIVITY	
		Rest period	Entire day	Rest period	Entire day
Wakeful	1	74	71	2.4	—*
	2	73	72	2.3	26
	3	78	63	4.5	23
Mean		75	69	3.1	25
Laboratory	1	37	42	5.7	35
	2	37	51	5.1	31
Mean		37	47	5.4	33

* Record incomplete.

Compensation for loss of sleep

Records of activity during respite from the wakeful regime were obtained for three animals drawn at random from the wakeful group, and comparable records were obtained for two animals from the laboratory group. These records were taken after the rats had lived under the experimental conditions for at least 50 days. They were obtained during the four-hour rest periods on four successive days and throughout the fifth day. In evaluating the records, the procedures and criteria which had previously been validated against direct observation were used.

The activity results are summarized in table 3. The table indicates that the rats which had been deprived of sleep took advantage of their rest periods, spending on the average 75 percent of the time in inactivity, whereas the controls were inactive only 37 percent of the time. When, on the fifth day, the wakeful rats were given a day of freedom from enforced activity, they rested 69 percent of the time while the controls were inactive 47 percent of the time. The experimental animals went through fewer cycles of activity and inactivity than did the controls.

When, at the end of the experiment, the groups were subdivided, and some of the rats were returned to the laboratory cages, it was noted that the rats which had been deprived of sleep were found asleep more frequently than were the controls. Most of the rats which had grown scrawny and thin under the wakeful regime recovered their sleek appearances and gained weight. It did not appear, however, that they would overtake their littermates which had been in the control groups.

Ability to withstand uninterrupted enforcement of wakefulness

Inasmuch as the wakeful rats had been forced to get along for 10 to 18 weeks with only four hours a day for sleep, the termination of the experiment presented an opportunity to make some observations concerning Hollingworth's theory that sleep is simply a habit (8). The wakeful rats had been given a good chance to inure themselves to loss of sleep. Therefore, rats were taken from each of the four groups to make up a new group of 48 subjects, and these were put on a 24-hour wakeful regime until they collapsed. It soon became evident that the rats which had been forced to adapt to partial deprivation of sleep were, if anything, less able than the controls to stand up under the stress of complete deprivation. The rats from the wakeful group collapsed in from 2 to 14 days, the controls in from 4 to 18 days.

CONCLUSIONS

On the basis of observations of four groups of white rats kept awake 12 hours, 16 hours, 20 hours, and 24 hours a day, it is concluded that the animals can adjust reasonably well to a regime which allows them four hours a day for sleep, but that they cannot endure total deprivation.

Further observations, on rats forced to be intermittently active 20 hours a day, lead to the conclusions that prolonged partial deprivation of sleep:

(1) Retards the growth of white rats;
(2) Makes them highly irritable and highly reactive;
(3) Does not impair ability to learn.

Finally, observations made after the experimental animals had been under the 20-hour regime for 10 to 18 weeks indicated that they had not "broken the habit" of sleep: they were no more able to withstand uninterrupted deprivation than were control rats. On the contrary, they appeared to need sleep and to take advantage of every opportunity to get it.

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